SEX-RATIOS AND THE EXTENT OF PARTHENOGENETIC REPRODUCTION IN SOME COLLEMBOLAN POPULATIONS

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Information about sex-ratios and the possible lack of males has considerable significance for understanding the dynamics and production ecology of natural populations. Thus, other things being equal, the reproduction of parthenogenetic pure female populations is expected to be twice as efficient as the reproduction of sexual populations composed of males and females in the usual 1 : 1 ratio. The reasons why sexual populations can exist in spite of this obvious advantage of asexual reproduction has recently gained renewed interest among population geneticists (Maynard Smith 1971, Ghiselin 1974, Williams 1975). In ecological studies, however, little attention has so far been paid to the relative distribution of sexes within natural populations and its significance for population dynamics and energy budgets.

In the case of Collembolan populations very little information about sex-ratios can be found in the literature. Most records available are summarized by Hüther (1961) who himself reported the sex-ratio of 22 species studied in German vineyards.

The existence of parthenogenetic reproduction in *Collembola* was until recently considered doubtful. An earlier paper (Petersen 1971) summarized the available evidence for parthenogenesis in Collembola and verified this mode of reproduction for two common Collembolan species *Tullbergia krausbaueri* (Börner) and *Isotoma notabilis* Schäffer. In this paper *Tullbergia krausbaueri* was reported as forming pure female populations in a Danish beech wood whereas populations of the same species found in a sand-dune area in N.W. Jutland proved to be bisexual.

The following will present the sex-ratios of a number of the most abundant Collembolan species in the soil and litter of a Danish beech wood and demonstrate the importance of parthenogenetic populations in this Collembolan community.

Further, it will be shown that bisexual and parthenogenetic populations of the same species can be found within short distances of each other. Some speculations will be presented as an attempt to explain the incidence of bisexual and parthenogenetic populations, respectively.

Estimation of the sex-ratio.

The sex-ratios in the present paper are expressed in terms of the number of males as a percentage of the total number of sexually identified specimens. After extraction by an efficient high-gradient extractor (Petersen 1978) all specimens were mounted on slides in the « Faure-Berlese » medium. All or a large representative proportion of individuals from each species were examined with a

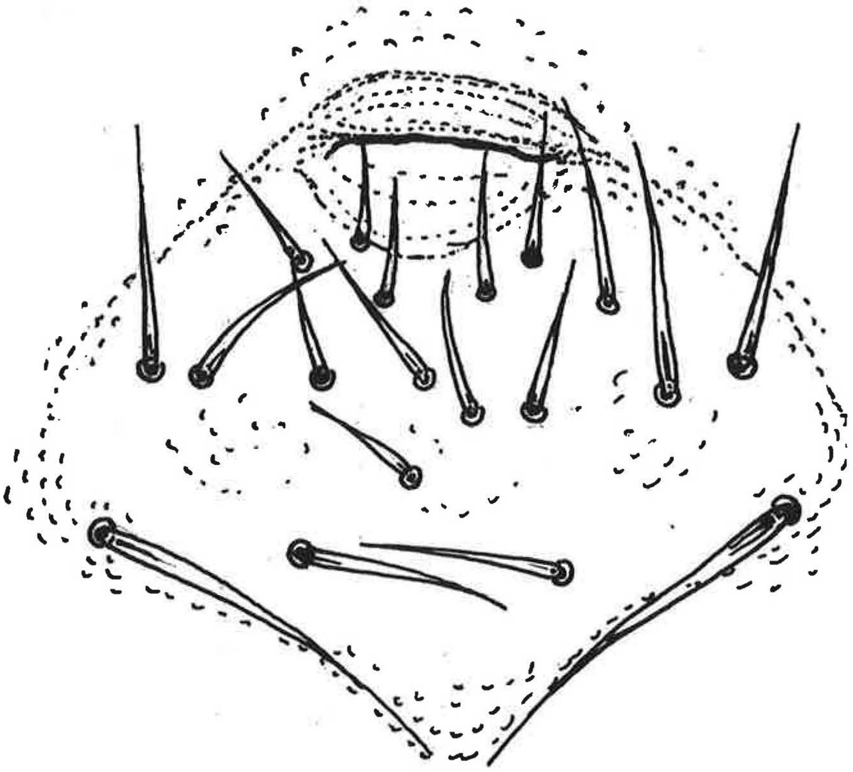

FIG. 1
Female genital area. « Closed ».
Folsomia quadrioculata (Tullberg).

view to identification as males, females or juvenile specimens. Further, the body length was measured by means of an ocular-micrometer.

Generally the shape of the genital aperture was used as a sex criterion. In females the aperture is transversally orientated (fig. 1, 2), whereas males have longitudinally orientated genital apertures (fig. 3, 4). In both sexes a more or less regular alternation between stages with « closed » (fig. 1, 3) and « open » genital apertures (fig. 2, 4) can be recognized. They seem to correspond to stages of sexual inactivity and sexual activity respectively.

In addition to the shape of the genital aperture the use of a phase contrast microscope often allows some genital structures to be seen internally in Collembolan bodies made transparent by the Faure-Berlese medium.

Thus, in females, densely packed spherical cells which make up the ovaries, or even fully-developed eggs, may be recognized. A large part of the body of males with « closed » genital apertures may be finely dotted or packed with filamentous structures (developmental stages of spermatogenesis). The testes of males with « open » genital apertures are composed of coarser vacuoles or have a more diffuse « flocculent » appearance. An ejaculatory duct is often clearly visible.

Schliwa (1965) explains the condition of the testes in the stages of sexual activity as connected with the secretion of spermatophore-stem material whereas spermatogenesis is confined to the stages of sexual inactivity.

Specimens without developed genital apertures were classified as juveniles. No morphological characters are known which make a sex identification possible for these juvenile specimens. In addition to the juveniles a number of individuals which have a larger body size than the smallest sexually developed specimens, and therefore classified as adults, have been impossible to sex because of their position on the slide, or because the genital apertures were concealed by the furca, gut contents etc.

The possibility of sex identification varies considerably between species. Thus, for instance, nearly all mounted specimens of *Onychiurus* and *Tullbergia* species may be sexed. The sex of *Folsomia* species is also relatively easily identified. On the other hand, the sex identification of especially *Tomocerus, Lepidocyrtus* and other Entomobryid species is made with considerable difficulty.

The inability to sex all adult individuals naturally lowers the accuracy of the sex-ratio estimate. What is worse, it cannot be excluded that the sex-ratio estimates in this way become biassed since the two sexes may not be equally safely identified. In table 1, which presents the sex-ratio estimates of some beech forest species, a column shows

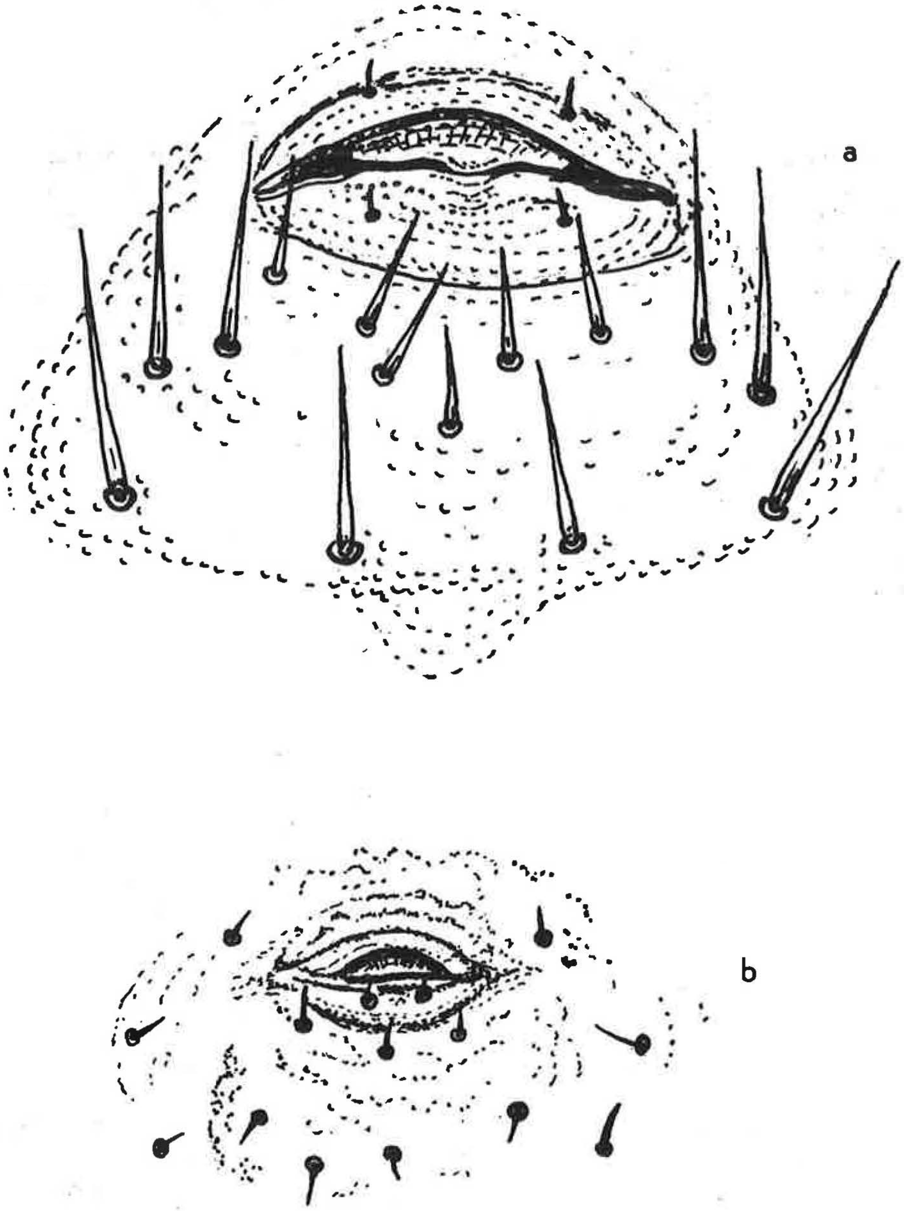

FIG. 2

Female genital area. « Open », lips developed.
a. *Folsomia quadrioculata* (Tullberg).
b. *Tullbergia* (*Mesaphorura*) *macrochaeta* Rusek.

the percent of specimens identified to sex in relation to the total number of adult specimens estimated on the basis of size measurements. This information provides the means to evaluate the sex-ratio estimates.

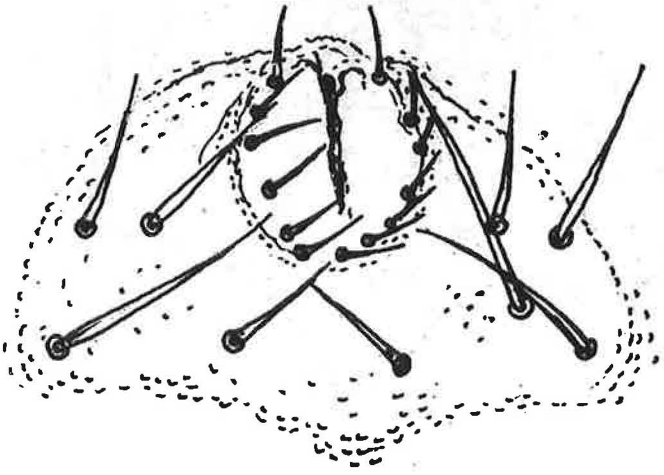

FIG. 3

Male genital area. « Closed ».
Folsomia quadrioculata (Tullberg)

Sex-ratios of the beech wood populations.

The study presented here is part of a more comprehensive investigation of Collembolan population and production ecology which is integrated in the Danish IBP beech forest ecosystem project. This multidisciplinary ecosystem study which is still only partly published (Thamdrup et al. 1975) was carried out in a pure c. 85 years old beech stand, Hestehaven at Kalö, E. Jutland (fig. 5). The soil is developed as a typical mull, and is through the vegetation period more or less completely covered by a field layer mainly composed of *Anemone nemorosa L.*, *Melica uniflora* Retz, and *Asperula odorata L.*

The *Collembola* fauna was sampled monthly through nearly two years. About 60 different species have been recorded within the research area of 1.5 hectares. The population density of the total Collembolan fauna of the litter layer and the uppermost 6 cm of the soil varied in 1970 between 26.000 and 66. 000 per m^2. The biomass varied in the same period between 76 and 160 mg d.wt. per m^2.

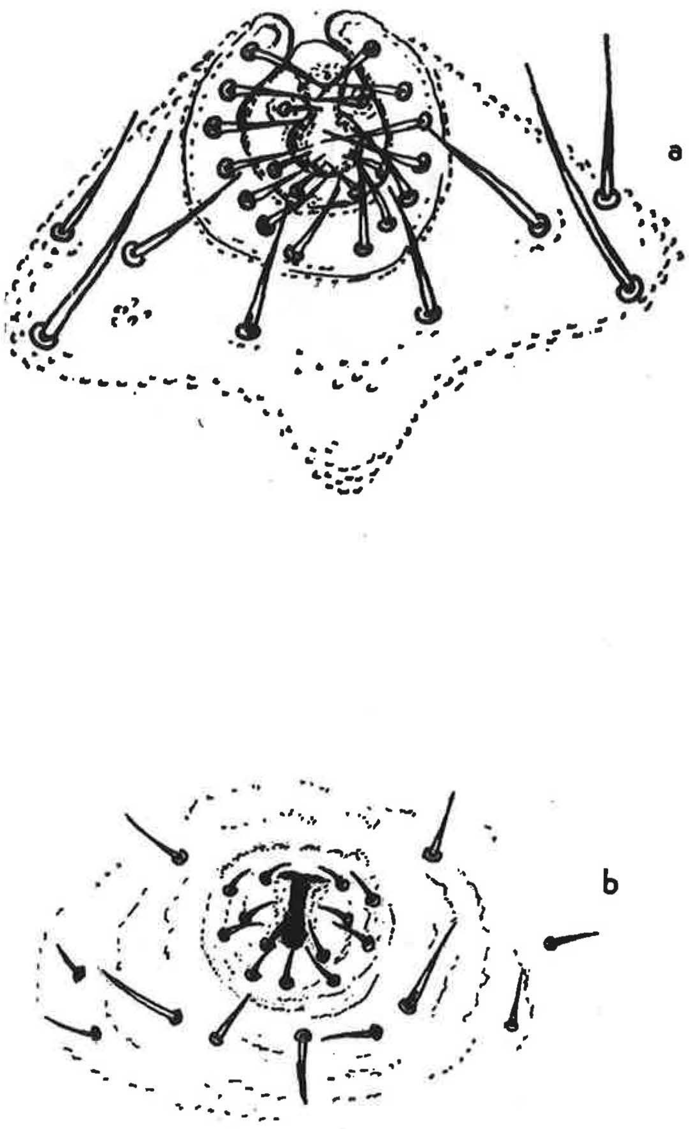

FIG. 4
Male genital area. « Open ».
a. *Folsomia quadrioculata* (Tullberg)
b. *Tullbergia* (*Mesaphorura*) *macrochaeta* Rusek.

Table 1 shows for some abundant species the sex-ratios presented as male percentages of the total number of individuals identified to sex. It appears from the table that males and females are about equally represented in the populations of *O. furcifer*, *T. flavescens*, *L. lignorum*, and *Dicyrtomina* spp.

TABLE 1

Male percentages in some abundant Collembolan populations of the Hestehave beech wood. (9 monthly samples February - November 1970. Litter and 0-6 cm soil horizon).

Species	Specimens identified to sex	sexed specimens % of adults	males % of sexed specimens
Willemia anophthalma Börner 1901 (sensu Hüther 1962)	219	34	0
Onychiurus furcifer (Börner 1901)	390	80	47
Tullbergia (*Mesaphorura*) spp. *)	1.234	47	0
Tullbergia callipygos Börner 1902	112	84	0
Folsomia quadrioculata (Tullberg 1871)	238	77	31
Folsomia nana Gisin 1957	744	64	34
Isotomiella minor (Schäffer 1896)	458	31	0
Isotoma notabilis Schäffer 1896	461	45	0
Tomocerus flavescens (Tullberg 1871)	229	55	45
Lepidocyrtus lignorum Fabricius 1775, Gisin 1964	153	16	42
Megalothorax minimus (Willem 1900)	409	83	0
Sminthurinus aureus (Lubbock 1862)	106	83	30
Dicyrtoma (*Dicyrtomina*) spp. **)	37	52	54

The taxonomy is based on Gisin (1960, 1964) and Hüther (1962)).

*) *Tullbergia* (*Mesaphorura*) spp. include the following species: *Tullbergia macrochaeta* (Rusek 1976), *T. krausbaueri* (Börner 1901) (sensu Rusek 1971), and *T. sylvatica* Rusek 1971.

**) *Dicyrtoma* (*Dicyrtomina*) spp. include specimens identified as *Dicyrtoma minuta* (O. Fabricius 1973), *D. saundersi* (Lubbock 1862) & *D. ornata* (Nicolet 1841) according to Gisin (1960). The identity of these forms as separate species is not certain.

The sex-ratio estimate may be considered relatively accurate for *O. furcifer* whereas the low percentages of adult specimens of *Lepidocyrtus* which could be identified to sex warns against attaching too much significance to the male percentage estimate of this species. Similarly, the male percentage of *Dicyrtomina* spp. may be of restricted value because it is based on the examination of a low number of specimens. In the populations of *F. quadrioculata, F. nana,* and *S. aureus* males seem to make up only about a third of the adult population, and are thus only half as abundant as the females. These estimates are probably relatively accurate. However, they do not necessarily result from an originally biassed sex-ratio of the offspring, but could equally well be explained from an assumption that the life-span is shorter for males than for females such as demonstrated for *Sminthurides aquaticus* (Bourl.) by Falkenhan (1932).

The most striking result which is apparent from table 1 is the total lack of males in several species. The evidence is based on a large number of individuals examined from a whole annual cycle, so although parthenogenetic reproduction has only been proved by culture experiments for *I. notabilis* and *T. krausbaueri* s.l. (Petersen 1971), there is little doubt that in addition to these species *W. anophthalma, T. callipygos, I. minor,* and *M. minimus* also reproduce exclusively parthenogenetically throughout the year in the Hestehave beech wood.

The taxonomy of *T.* (*Mesaphorura*) *krausbaueri* (Börner) has recently been revised by dr. J. Rusek, Praha (Rusek 1971, 1974, 1975, 1976). Dr. Rusek kindly examined a part of my *Tullbergia* material and was able to demonstrate at least 4 separate species among the specimens previously (Petersen 1971) identified as *T. krausbaueri,* i.e. *T.* (*Mesaphorura*) *macrochaeta, T.* (*M.*) *krausbaueri* s. str., *T.* (*M.*) *sylvatica,* and *T.* (*Wankeliella*) *peterseni* (Rusek 1975). Among these species *T. macrochaeta* appears to be the most abundant followed by *T. sylvatica. T. krausbaueri* and *T. peterseni* are rather rare in the Hestehave site. No males have been found among the large number of specimens examined belonging to this composite group of species, so in the Hestehave site parthenogenesis may safely be assumed as the obligatory mode of reproduction in at least the two most common forms (*T. macrochaeta* and *T. sylvatica*).

In addition to the abundant species shown in table 1 the following less frequent species may with some degree of certainty be counted among the parthenogenetic species in the Hestehave wood:
Willemia aspinata Stach 1949
Onychiurus absoloni (Börner 1901)
O. serratotuberculatus Stach 1933
Tullbergia denisi (Bagnall 1935)

Folsomia cf. monosetosa Rusek 1966
F. candida (Willem 1902) s. Lawrence 1973

Thus 7 abundant species and probably a total of not less than 15 species are maintained in the research site of the Hestehave wood as parthenogenetic, pure female populations. As shown in table 2 the pure female populations of the common species amount together to 72% of the annual mean density and 22% of the annual mean biomass of the total Collembolan population.

TABLE 2

Abundant Collembolan species existing as pure female populations in the Hestehave beech wood. Litter and 0-6 cm soil horizon. (December 1969 - November 1970). (see footmarks of table 1).

Species	Relative density % of total Collembola	Relative biomass % of total Collembola
Willemia anophthalma	1.8	.4
Tullbergia (Mesaphorura) spp.	36.0	5.6
T. callipygos	1.6	3.0
Isotomiella minor	21.2	7.6
Isotoma notabilis	7.0	2.7
Megalothorax minimus	4.3	2.2.
Sum	71.9	21.5

It is therefore concluded that parthenogenetic populations contribute significantly to the composition of at least this particular Collembolan community. The great difference between their contribution in terms of density and biomass respectively clearly illustrates that the parthenogenetic mode of reproduction especially characterizes the smallest Collembolan species.

This again correlates with the fact that the parthenogetic populations show a much stronger dominance in the mineral soil horizons than in the litter layer. In fact, all the parthenogenetic species except *Isotoma notabilis* may be classified as the typical eu-edaphic life forms as described by Gisin (1943).

Sex distribution in various populations of Tullbergia macrochaeta.

In a previous paper on parthenogenesis in Collembolan populations (Petersen 1971) the discovery of a bisexual population of *Tullbergia krausbaueri* (Börner) s.l. from wind-exposed sand-dunes at the West-coast of Jutland was reported. Later, members of a similar bisexual population were extracted from the rhizosphere of *Ammophila arenaria* (L.) at the beach belonging to the Molslaboratory, which is situated about 10 kms from the Hestehave beech wood dealt with above (fig. 6).

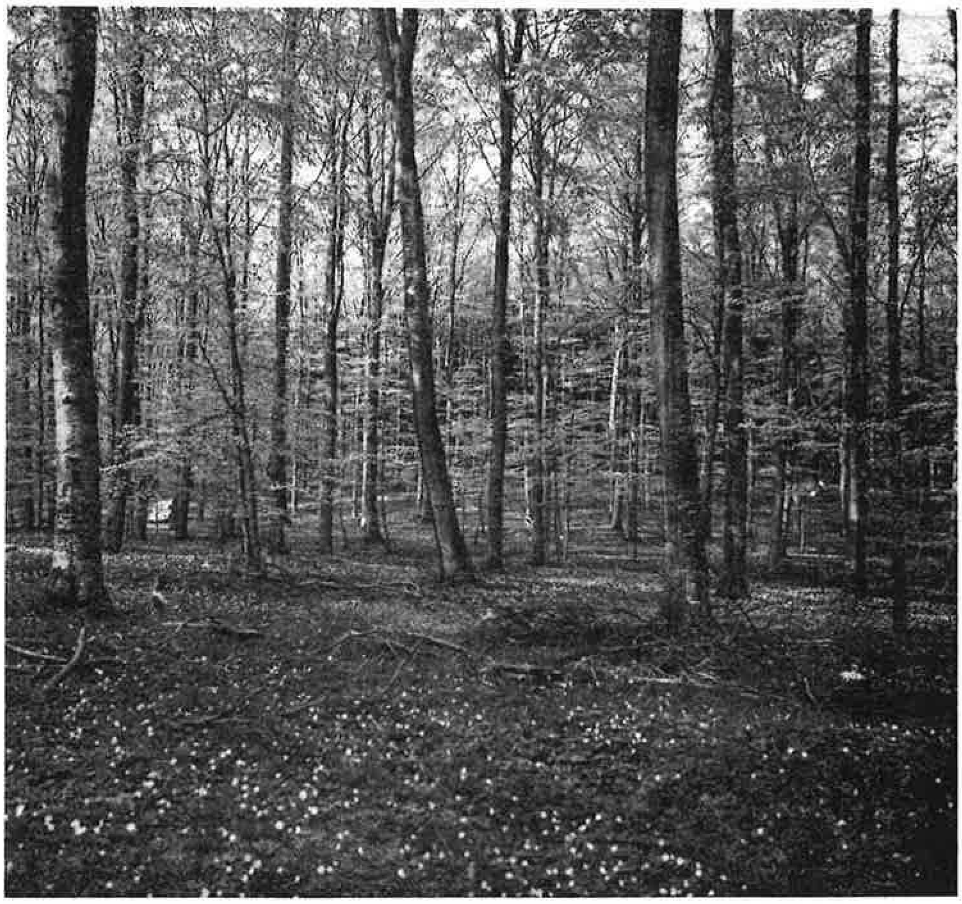

FIG. 5
The Hestehave beech wood. Early spring.
(Merete Thaarup Jepsen phot.)

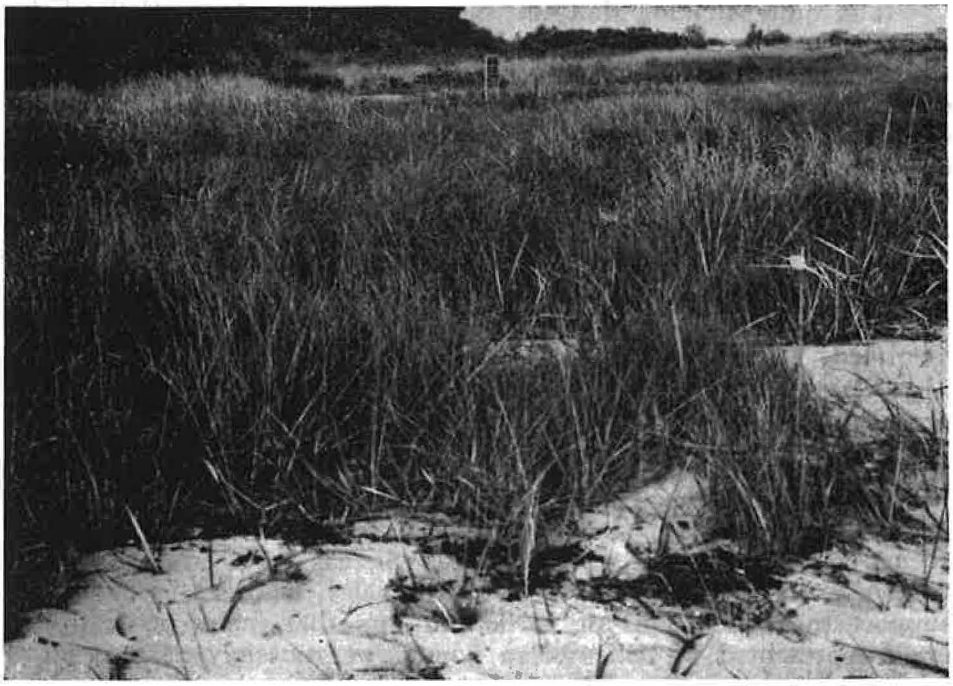

FIG. 6
The beach at the Molslaboratory.
Outer zone with *Ammophila arenaria* (L.).

After dr. Rusek's revision of the *Tullbergia* genus (see above) he also examined the material collected from the beach sites. The examination proved that the bisexual species from the beach habitats is identical to the most abundant *Tullbergia* species in the Hestehave wood, i.e. *T. macrochaeta,* which exists there as a permanent pure female population.

The examination of samples taken along transects from about 10 m from the shore-line where the *Ammophila* vegetation begins to about 80 m from the shore-line indicated that a bisexual population including about 30% males extends inland at least as far as 36 m from the shore-line. However, samples taken at a distance of c. 50 m from the shore-line and further inland included the same species, exclusively represented by females. Between 40 and 50 m from the shore-line the vegetation changes from the typical sand-beach community dominated by e.g. *Ammophila arenaria* to a heathland community dominated by e.g. *Deschampsia flexuosa* (L.) and *Calluna vulgaris* (L.)

It is quite striking that the species diversity of the Collembolan community increases considerably from the outer *Ammophila* zone where the bisexual population is found to the inner *Deschampsia* - *Calluna* zone, where the *T. macrochaeta* population appears to be parthenogenetic. *T. macrochaeta* represents the only *Tullbergia* species found in the outer zone, whereas two other *Tullbergia* species have been found in the same sample units as *T. macrochaeta* in the inner zone.

In a *Calluna*-dominated heathland vegetation about 1 km inland from the beach *T. macrochaeta* was also recorded as a pure female population. Here at least one additional species of *Tullbergia* was identified.

Discussion.

The average sex-ratios of some abundant bisexual species in the Hestehave beech wood showed for a few species (*O. furcifer*, *T. flavescens*) equal number of the two sexes, whereas males in other species were about half as numerous as the females. Hüther's (1961) results support the conclusions of earlier authors that males generally are under-represented in Collembolan populations possibly as a result of a shorter life-span than the females.

Thus, in many species males made up less than half the female population. For some, especially among the *Tullbergia* species, a very low proportion of males was recorded, or males were absent as in e.g. *Tullbergia quadrispina* or *Isotomodes productus*. Hüther doubted that different life-spans could explain the examples of total absence of males and suggested parthenogenetic reproduction as a likely explanation although no certain examples of parthenogenesis in *Collembola* had been demonstrated at that time.

The examples of populations in the Hestehave beech wood where males constitute about a third of the adult population (*F. quadrioculata*, *F. nana*, *S. aureus*) may possibly be explained as the result of different adult life-spans. However, several examples of abundant species in which no males have been found can only be explained if a parthenogenetic (thelytokous) mode of reproduction is assumed. For two of these species this assumption has been supported by means of culture experiments (Petersen 1971).

Seven of the most abundant species in the Collembolan community of the Hestehave beech wood which together amounts to 72% of the total Collembolan density thus exist as apparently obligatory parthenogenetic populations. Such importance of parthenogenesis in *Collembola* is in contradiction to the conclusions of Schaller (1953) and Mayer

(1957) who explicitly doubted the existence of parthenogenesis in *Collembola,* and explained earlier records of reproduction by isolated females as the result of accidental introduction of spematophores with the food.

It should be emphasized that Schaller and Mayer only worked with the larger Collembolan species. Thus, Schaller's pioneer work with the first description of indirect sperm transfer in *Collembola* dealt with *Tomocerus vulgaris* (Tullberg) and *Orchesella villosa* (Geoffroy). Mayer supplemented the list of species examined with several others including the eu-edaphic forms *Onychiurus armatus* (Tullberg) and *Tullbergia quadrispina* (Börner). However, these two species are much larger than the most common eu-edaphic species found in the Hestehave wood which appear to represent the type of *Collembola* especially characterized by parthenogenetic reproduction.

Since Schaller's and Mayer's work parthenogenesis has been proved to exist at least facultatively in *Hypogastrura matura* (Folsom), (Christiansen 1964), *Onychiurus hortensis* Gisin (Choudhuri 1958), *Tullbergia krausbaueri* (Börner) s.l. (Hale 1966, Petersen 1971), *Folsomia candida* (Willem) (Goto 1960, Marshall & Kevan 1962, Green 1964, Husson & Palévody 1967), *Isotoma notabilis* Schäffer (Petersen 1971), and *Cyphoderus javanus* (Kurup & Prabhoo 1977).

The addition of species for which large pure-female samples have been reported (Hüther 1961, Petersen 1971, and the present paper) brings the number of known and likely obligatory or facultatively parthenogenetic Collembolan species up to about 25, most of which conform with the eu-edaphic life-form as described by Gisin (1943). It is therefore concluded that parthenogenesis constitutes a significant mode of reproduction in eu-edaphic *Collembola.*

The discovery that one of the most abundant parthenogenetic species in the Hestehave beech wood *Tullbergia macrochaeta* (Rusek 1976) exists as bisexual populations in dunes and sandy beach habitats, and that pure female populations may substitute bisexual populations of the same species within a distance of 15 m corresponding to the division between two vegetational zones of the beach, invites consideration of the significance of different types of reproduction in an ecological context.

Can we explain why sexual reproduction is maintained in one population, when parthenogenesis has become obligatory in another population of the same species? This is essentially the same question which has occupied population geneticists for many years: How can sexual reproduction persist when it is evident that the transfer of genes to the next generation is 50% less efficient in comparison with an asexual mode of reproduction? The question has recently gained renewed interest stimulated by publications of e.g. Maynard Smith (1971), Ghiselin (1974), and Williams (1975). In his book « Sex and Evolution » Williams (1975) argues convincingly for the view that sex is an adaptation to unpredictable conditions. The progeny of sexual parents extend to higher values of fitness dosage than asexually produced progeny because of greater variability between the sexually produced individuals. Sexually produced progeny will have an advantage when selection is so strong that only individuals in the uppermost end of the fitness dosage scale have a chance of survival and reproduction.

Without going into a theoretical discussion of this problem it is interesting to note that the occurrence of bisexual and parthenogenetic populations of *Tullbergia macrochaeta* seems to support Williams' hypothesis. The environmental conditions in the beech wood soil are probably relatively stable and predictable, at least in comparison with the conditions in the sparse *Ammophila* vegetation growing in loose beach sand which is subjected to occasional disturbances by wave and wind action.

There might also be a limit to the ability of closely-related sexual species to discriminate beteen each other's spermatophores. Little is known about how the Collembolan females recognize the sparmatophores of their own species, but it is possible that the danger of cross-fertilization between species would exclude the existence of the many closely-related species found in the woodland soil if they were dependent on sexual reproduction by means of the indirect spermatophore transfer mechanism.

Finally, the success of an indirect spermatophore transfer is probably dependent on a rather dense population for the females to have a chance of finding the spermatophores. In the beach sand habitat the *Tullbergia* populations seem to be closely associated with the rhizosphere of the beach plants, and the specimens are therefore forced together in rather dense populations which makes indirect sperm transfer possible. In the beech wood soil, however, the specimens of the individual populations are more evenly distributed. On the large surface of the soil interstices it is not unlikely that the chance of an encounter between a Collembolan female and spermatophores of her own species may be too small to secure a successful reproduction.

Summary.

The study of the Collembolan community in a Danish beech wood has demonstrated for a number of the larger Collembolan species that males constitute from about a third to about a half of the adult population. Seven of the most abundant smaller species, however, can safely

be attributed a parthenogenetic (thelytokous) mode of reproduction which in these particular populations appears to be obligatory. At least 8 additional species which are less common in the beech wood site are probably also parthenogenetic.

Parthenogenetic populations seem to be especially characteristic of the species conforming to the eu-edaphic life-form, and they are more important in the soil than in the litter layer. The pure female populations of the abundant species constitute together 72% of the annual mean density and 22% of the annual mean biomass of the total Collembolan population and are therefore considered a significant element of the Collembolan community.

Tullbergia macrochaeta (Rusek 1976) is found as pure female populations in the beech wood, in a *Calluna heathland,* and in the inner vegetational zone of a sandy beach, but as a bisexual population in the outer zone of the same beach. The two beach populations are separated by less than 15 m. The occurrence of bisexual and parthenogenetic populations of *T. macrochaeta* supports the idea of sex as an adaptation to unpredictable environments (Williams 1975). Some other hypotheses are suggested with a view to explaining the distribution of sexual and parthenogenetic populations.

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SUMMARY

Sex-ratios are presented for some abundant Collembolan species in a Danish beech wood. Male percentages vary from c. 30% to c. 50% of the adult population in some larger species, whereas several smaller, mainly eu-edaphic, species exist as pure female populations. 7 abundant parthenogenetic species constitute together 72% of the annual mean density, and 22% of the annual mean biomass of the total Collembolan population. At least 8 additional species are probably also parthenogenetic. *Tullbergia macrochaeta* (Rusek 1976) forms both parthenogenetic and bisexual populations. A bisexual population is found in the outer zone of a sandy beach separated by less than 15 m from a pure female population of the same species. A discussion is presented with a view explaining the distribution of sexual and parthenogenetic populations.

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